Additional fossil plants from the Drybrook Sandstone, Forest of Dean, Gloucestershire

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Synopsis

New ovules are described showing sufficient internal structure to make them referable to *Carpolithus* Schlotheim, 1820, although as a new species *C. puddlebrookense.*

Lepidophyte stems previously called *Scutellocladus variabilis* are redescribed as being persistently leafy, ligulate and as having infrafoliar bladders. These characters make the stems referable to *Tomiodendron* Radczenko, emend. Meyen 1972. They are therefore rediagnosed as *T. variabilis* (Lele & Walton) comb. nov.

Introduction

The shale bed in the Drybrook Sandstone in Hazel Hill Quarry, near Puddlebrook, Forest of Dean is a well known locality of fossil plants. Allen (1961) described *Lepidostrobophyllum fimbriatum* Kidston from here while Lele & Walton (1962) described the rest of the then known flora of macrofossils and spores. More recently the moss *Muscites plumatus* Thomas (1971) has been found here. The miospore flora of the Drybrook Sandstone has also been investigated by Sullivan (1964) and shown to be comparable to that of the Oil Shale group of Scotland. The inference from this is that the Drybrook flora is of lower Upper Viséan age.

The present account deals with material that has been collected from the locality over many years. The very few specimens found indicate the relative scarcity of these plants in the shale bed. All the specimens are in the collections of the Palaeontology Department of the British Museum (Natural History).

Systematic descriptions

Division SPERMATOPHYTA

Form-genus *CARPOLITHUS* Schlotheim, 1820

Carpolithus puddlebrookense sp. nov.
Figs 1–3

Description. Four isolated ovules have been found from the Drybrook Sandstone of Puddlebrook Quarry. All are preserved as partially flattened casts with very little of their carbonized compression material having survived fossilization. They are virtually identical in size, being 4 mm in length and 2 mm in maximum width. Three have been split, on breaking the shale, showing the integuments to be 0·33 mm thick and fused to the nucellus except at the apex where they divide into four apical lobes. The possession of separate integumental lobes naturally precludes the possession of a micropyle, but one specimen (Figs 1, 2) shows signs of a salpinx with an underlying lagenostome and plinth. None shows any signs of integumental tissue differentiation into sarcotesta and sclerotesta but this is to be expected due to the limitations of preservation.

The four integumental lobes appear to be equal in size and therefore suggest that the ovules were originally radially symmetrical. Slight indications can be seen of longitudinal

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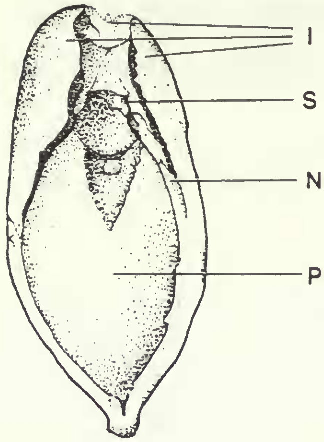

Fig. 1 *Carpolithus puddlebrookense* sp. nov., **holotype** V.60509a, × 15. I, integuments. S, salpinx. N, nucellus. P, prothallus.

ridges on the main body of the ovule which pass upwards into the free integuments. Two of the specimens possess short pedicels, 0·3 mm long, but none are attached to any other plant structure. Cellular details are not visible on any part of the ovules other than indications of longitudinal files of cells on the integument and nucellus. Two of the ovules appear to have a triangular mark projecting down from the apex of the nucellus, but this could be a preservation effect or the result of shearing strains as the rock was broken. These two ovules also show a marked depression which may indicate the area bounded by the lagenostome.

Compressions and casts of seeds are very difficult to assign to any genus with certainty. Crookall (1976) has reviewed these Carboniferous genera but persists in including many within the ill-defined genus *Carpolithus* Schlotheim, 1820. If the Drybrook specimens are to be given a name then it is within this genus that they are probably best included. The only species that are of comparable size are *C. ellipticus* Sternberg, *C. granulatus* Sternberg, *C. perpusillus* Lesquereux and *C. pseudosulcatus* Crookall, but they are all known only from the Westphalian and are themselves ill-defined. Crookall (1976) does describe his *Carpolithus* sp. A and sp. B from the Viséan but they are much larger than the present specimens. The Drybrook ovules are also similar in size to those included in *Lagenospermum* Nathorst, but they are more ovoid in shape and lack the longitudinal ribbing characteristically found on *Lagenospermum*.

The present ovules also show similarities to certain petrified ovules described by Long and other workers from the Calciferous Sandstone (Cementstone Group) of Berwickshire. They can be clearly included within the order Lagenostomales as outlined by Seward (1917) and modified by Long (1975). The possession of four integumental lobes, which are free only above the nucellus apex, and a distinct salpinx suggests that they could be included within the family Eurystomaceae. The closest genus of radially symmetrical ovules is *Eurystoma* Long 1960 emend. 1975 which has two species. *E. angulare* Long 1960 is the closer of the two to the present material, being comparable in size (4–8 mm long and 1–2·5 mm in maximum width) and in having four free apical lobes. The ovules, however, have much more prominent longitudinal keel-like ridges than those seen on the Drybrook specimens, giving them a squared outline when seen in transverse section. *E. burnense* Long 1975 is smaller (maximum size 5 × 3·5 mm) and is triangular in section with three very prominent wing-like ridges. Long has however shown that in the mature seed condition the keels decay or are eroded to give an almost circular outline in cross-section. The Drybrook ovules also differ from both these species in having less of a constriction of the level of division into free integumental lobes. However, it must be remembered that comparisons are being made between ovules which have been preserved in different ways. Longitudinal ridges and constrictions might easily have become less distinct during compression in the Drybrook shales.

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Figs 2–3 *Carpolithus puddlebrookense* sp. nov. Fig. 2, **holotype** V.60509a, × 20. Fig. 3, associated plant organ, V.60509b, × 20.

These differences, however, hardly seem sufficient for generic distinction unless one decides that the different types of preservation preclude such a close comparison being made. This is clearly the crucial point of the identification. We are inclined to take the view here that it is not absolutely certain in this case, so the Drybrook specimens are described here as a new species under the name *Carpolithus puddlebrookense* sp. nov.

DIAGNOSIS. Oval radiospermic ovules. Length 4–8 mm, maximum diameter 2·5 mm. Integument 0·13 mm thick, fused to nucellus except above its apex where it is divided into four lobes 3 mm long. Diameter of salpinx about 0·3 mm.

HOLOTYPE. V.60509a. Figs 1, 2.

PARATYPES. V.60509b (Fig. 3), V.60510.

LOCALITY. Hazel Hill Quarry, Puddlebrook, Forest of Dean, Gloucestershire, England; National grid ref. SO 646184.

HORIZON. Drybrook Sandstone; lower Upper Viséan.

DISCUSSION. The decision to include the ovules in *Carpolithus* is supported by other evidence. Although the Drybrook specimens are very similar to *Eurystoma* on the evidence of their general morphology, the natural affinities of the two groups of seeds is possibly rather doubtful. Long has shown that his seeds were borne in a loose branching system interpreted as a primitive cupule and he suggested that the parent plants were of the frond type described as *Alcicornopteris* Kidston (Long 1969). No such branching cupules, nor fronds of the *Alcicornopteris* type, have been described from the Drybrook Sandstone and I have seen no suggestions of any while collecting there. Cupule-like structures, however, have been found and described as *Calathiops* sp. by Lele & Walton (1962 : pl. 21, figs 27–29) although the relationship of these to the seeds is as yet unknown. They are rather different from those cupules described by Long, being much more robust with the cupular lobes fused for nearly their whole length.

One other associated plant organ, on nos V.60509a and b (Fig. 3), may also have some affinity with the seeds. It has a short pedicel which is expanded into a broad head with four apical points. However, we have no firm suggestion to make about its structure or function.

Division **LYCOPHYTA**

Genus ***TOMIODENDRON*** Radczenko, 1956 emend. Meyen, 1972

Tomiodendron variabilis (Lele & Walton) comb. nov., emend.
Figs 4–14

DESCRIPTION. *Scutellocladus variabilis* was briefly described by Lele & Walton in 1962 as part of their study of the Drybrook Sandstone flora. Since then, however, many more detailed accounts have been published of other Lower Carboniferous lycophytes, so this species warrants critical re-investigation. Lele & Walton's material therefore has been re-examined together with many new specimens from the same locality.

The majority of stem fragments are preserved only as impressions and very few retain any fragments of compressed plant material. The stems at first sight appear to be quite varied, but careful study revealed them to be all of the same general form. It was the splitting of the rock that controlled how the stem was exposed in many different ways. There are theoretically many surfaces that may be visible as a result of rock splitting along different planes and most can be seen on the various specimens available to us (Fig. 4). The stems are unbranched, except for a few that dichotomize, are up to 13 cm long and range in width between 0·2 and 2 cm. Leaves can be clearly seen attached to some of the stems (Fig. 6). They are spirally arranged, about 1 cm long and 2 mm broad, falcate in outline with acutely pointed apices. Many show a slight central ridge which we interpret as a leaf vein.

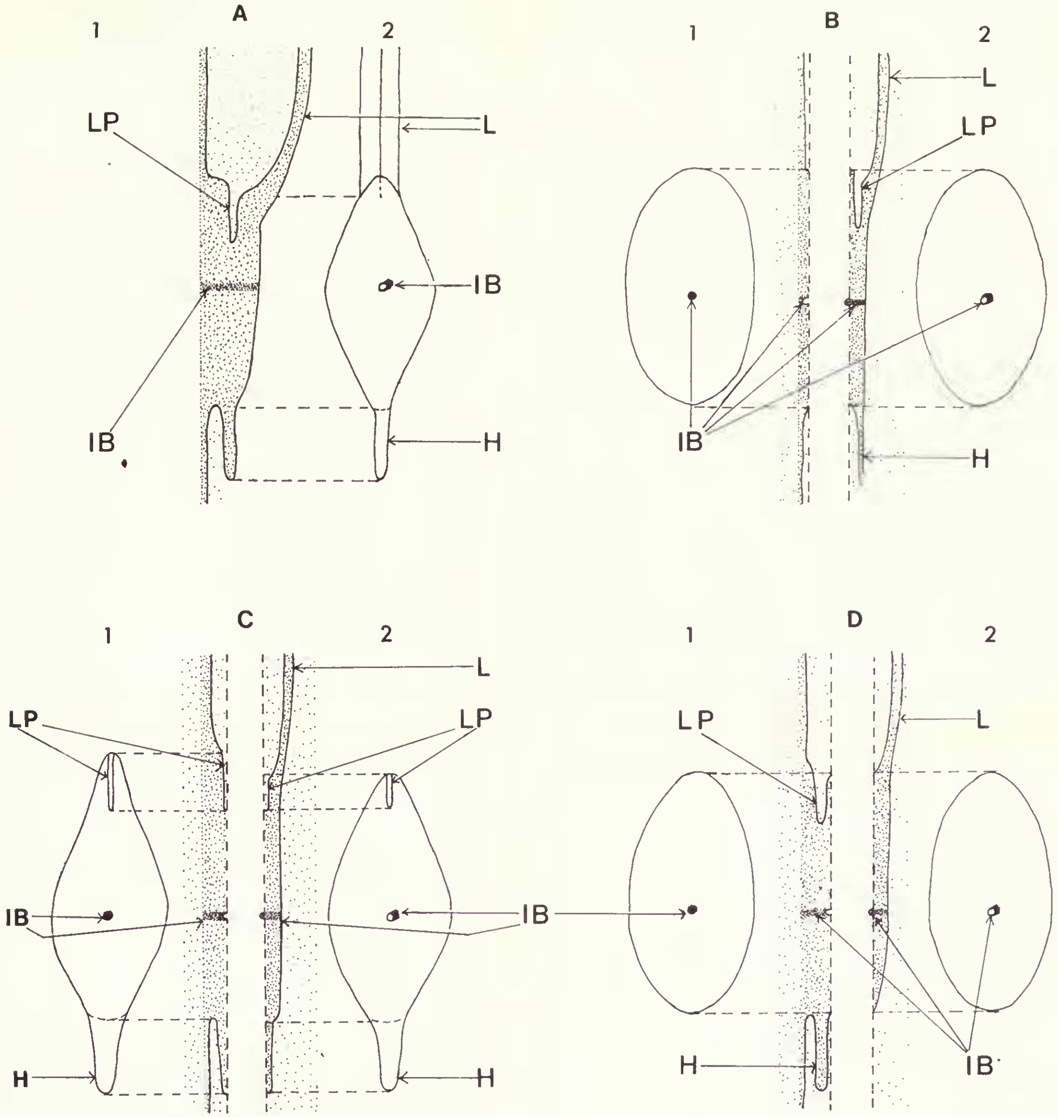

Fig. 4 *Tomiodendron.* Diagram to illustrate inter-relationships between preservation and fragmentation. Leaf cushions are illustrated in different aspects of exposure. The different preservation polymorphs are related to the ways that the matrices fractured to reveal the stems. Example A shows a situation where the fracture plane occurs at the surface of the compression, whereas B, C and D are cases where the fracture lines have sheared through the compression. Very little evidence is ever seen of leaf laminae, but heels are more often exposed (as in A2, C1 and C2). Ligule pits are also only sometimes seen (as in C1 and C2). The nature of the marks left by the infrafoliar bladders are consistent; they always collapsed inwards during preservation. They are illustrated here as infrafoliar projections on the right of the pairs, and as depressions on the left of the pairs of preservation polymorphs. In each example the central shaded part is an imaginary section, and the shapes at either side show the appearance of the fracture surface on the exposed rock surface. H — heel, IB — infrafoliar bladder, L — leaf, LP — ligule pit.

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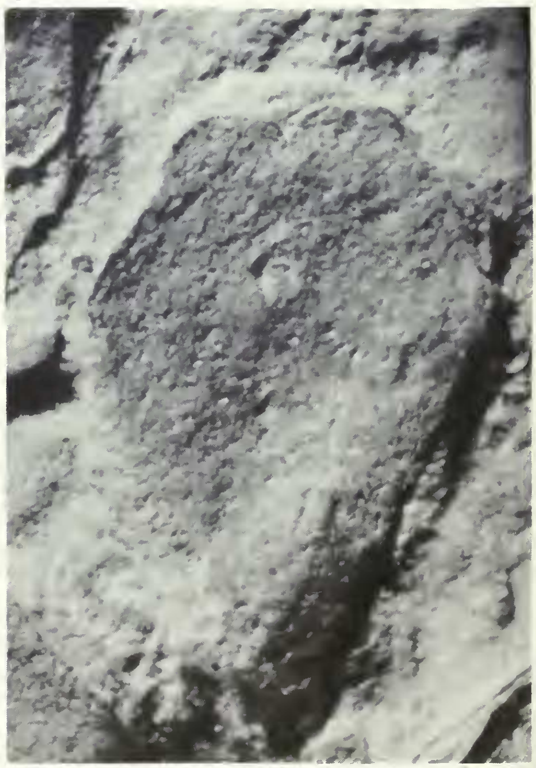

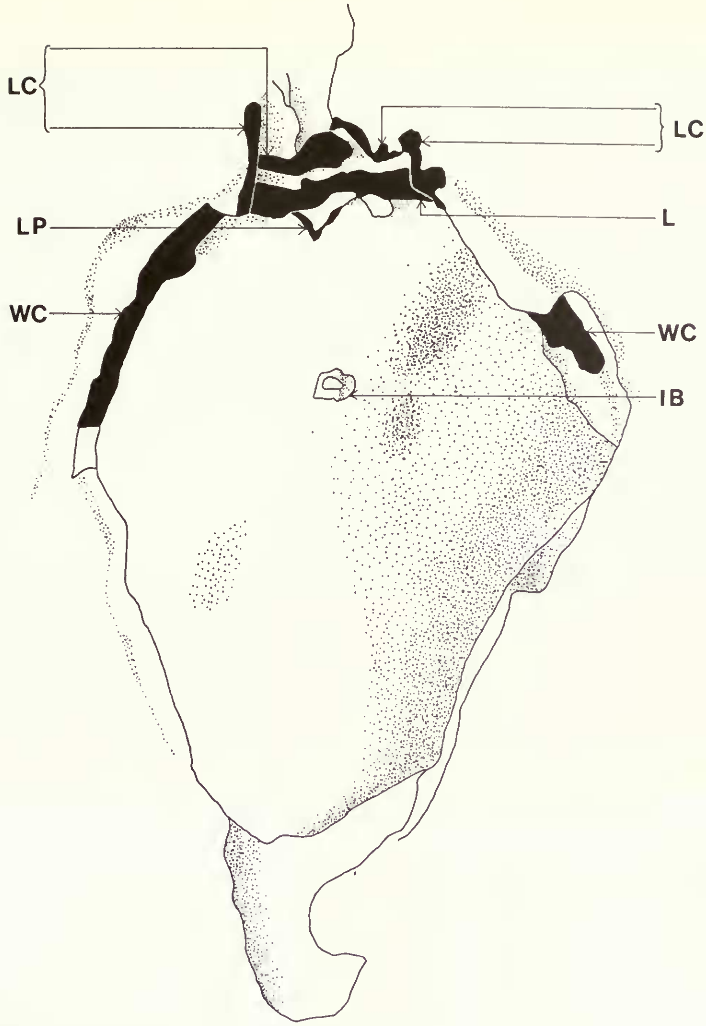

Fig. 9 *Tomiodendron variabilis.* Leaf cushion impression showing remains of leaf, wing, and ligule pit compression material. The upper angle of the leaf cushion and the base of the leaf lamina were uncovered by degaging. This specimen exhibits the type of fracture surface shown in Fig. 4, C2. IB, infrafoliar bladder. LC, compression of apical portion of leaf cushion. L, leaf lamina compression. LP, ligule pit. WC, wing compression. V.60346, ×25.

Many stems appear to have lost their leaves, instead having ovoid to rhomboidal scar-like outlines (Fig. 5). However, we interpret these as impressions of swollen leaf bases and believe that the leaf laminae were either not preserved during fossilization or were mechanically separated and lost during the splitting of the rock.

The swollen leaf bases can be described as leaf cushions for the reason given below. The ovoid leaf cushions are generally found on twigs less than 1 cm broad, are about 2 × 1 mm

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Figs 5–8 *Tomiodendron variabilis* (Lele & Walton) comb. nov. Fig. 5, leafless stem showing dichotomy, V.60223, ×2. Fig. 6, leafy stem, V.60350, ×2. Fig. 7, stem with rhomboid leaf cushions (compare with Fig. 4, A2 and C2), overlain by one with oval leaf cushions (compare with Fig. 4, Al, Bl and/or Dl), V.60346, × 4. Fig. 8, rhomboid leaf cushion with ligule pit cast (enlargement of Fig. 7), V.60346, ×20.

to 2·75 × 1·5 mm in size and separated by about 0·5 mm to 1·5 mm of stem surface (Fig. 7). The virtually symmetrical rhomboidal cushion outlines are up to 5 × 3·5 mm in size and about 0·5 mm to 1·5 mm apart (Figs 7, 8). Changes in density and dimensions of leaf cushions do however occur on some stems. Sunken leaf cushions, which we interpret as impressions of the outer surface of the stem, often have carbonaceous compression material around their edges disappearing into the matrix. Careful degaging reveals this to represent lateral extensions of the cushions similar to the wings described in *Tomiodendron* sp. and *Angarodendron leclerquianus* by Meyen (1976). Some of the sunken cushions also have carbonaceous compression material extending into the matrix at their lower angles, while others show extensions of the cushion depressions into short shallow grooves. From this evidence we conclude that the cushions had small heels.

Ligule pit casts are present in the upper angles of many leaf cushion impressions (Figs 8, 12), although their presence seems to depend on the way the rock split rather than on their actual preservation. The pit casts are roughly triangular in outline, with apertures 0·5 mm wide, and varying in length between 0·2 and 0·33 mm. Leaf laminae can usually be seen as lines of compression material running across the leaf cushion immediately above the apertures of the ligule pits (Fig. 9).

Some stem impressions are preserved in such a way that their leaf cushions are shown to extend into a rounded apex above the line of attachment of the leaf lamina. This subapical attachment of the leaf lamina leads us to describe the swollen leaf bases as leaf cushions even though leaf abscission does not occur. If the lamina was attached apically to the swollen leaf bases making the leaf attachment decurrent it would be more suitable to call them leaf bases. Many leaf cushions have a single, circular depression or projection which again needs to be interpreted in the knowledge of the type of stem preservation. Projecting cushions seen as in

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Figs 10–11 *Tomiodendron variabilis*, infrafoliar bladders. Fig. 10, leaf cushions with infrafoliar projections (compare with Fig. 4, B2 and D2), V.60344, ×10. Fig. 11, leaf cushion with infrafoliar depression (compare with Fig. 4, C2), V.60346, ×20.

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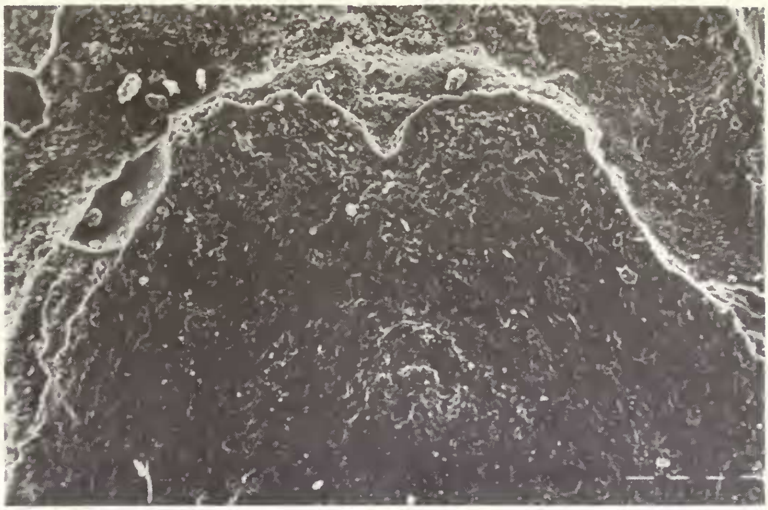

Fig. 12 *Tomiodendron variabilis*. Leaf cushion and ligule pit cellular detail (displayed using scanning electron microscope), V.60346, ×30.

life have depressions, while cushion impressions have projections. Similar, but larger, structures have been described as infrafoliar bladders in *Tomiodendron* by Meyen (1976) (Figs 10, 11).

Cellular detail can be seen on some leaf cushion surfaces using a binocular microscope, so latex moulds were prepared for observation with the scanning electron microscope. Cells about 30 × 15 μm in size were visible along the axis of the leaf cushion (Fig. 12). No stomata were seen but it should be remembered that the cellular detail was generally poor. Cuticle was also prepared from small fragments of compression taken from intercushion areas of a stem. All the cells were similar, being polygonal, slightly elongated towards the cushions and measuring about 30–40 × 15–20 μm with anticlinal walls 10 μm thick. No stomata were visible (Figs 13, 14).

COMPARISON. The Puddlebrook species was clearly a ligulate lycophyte stem although we have no idea of the size to which the plants grew. Many other genera of Lower Carboniferous lycophytes are similarly only imperfectly known, although many exhibit features closely comparable with some of our stems. Therefore we will confine our attention to those ligulate stems which are of comparable size. They are *Tomiodendron* Radczenko emend. Meyen 1972, *Angarodendron* Zalessky emend. Meyen 1976, *Ursodendron* Radczenko emend. Meyen 1972, and *Eskdalia* Kidston emend. Thomas 1968.

Russian Lower Carboniferous species of *Tomiodendron* have been described by Meyen (1972, 1976) and Gorelova (1978). Their descriptions of the leaf cushions lead to the conclusion that the genus *Scutellocladus* may be regarded as synonymous with *Tomiodendron*. The British specimens are, however, sufficiently different from all the Russian ones to be kept as a separate species and named *Tomiodendron variabilis* (Lele & Walton) comb. nov. (Table 1).

Angarodendron obrutschevii Zalessky emend. Meyen was originally diagnosed as eligulate, as was *T. variabilis*, although it is now known to be ligulate. *Angarodendron* did, however, shed its leaves and also has much larger infrafoliar bladders that sometimes occupy more than half the cushion width.

Ursodendron is very similar in its leaf cushion morphology but always has its cushions in

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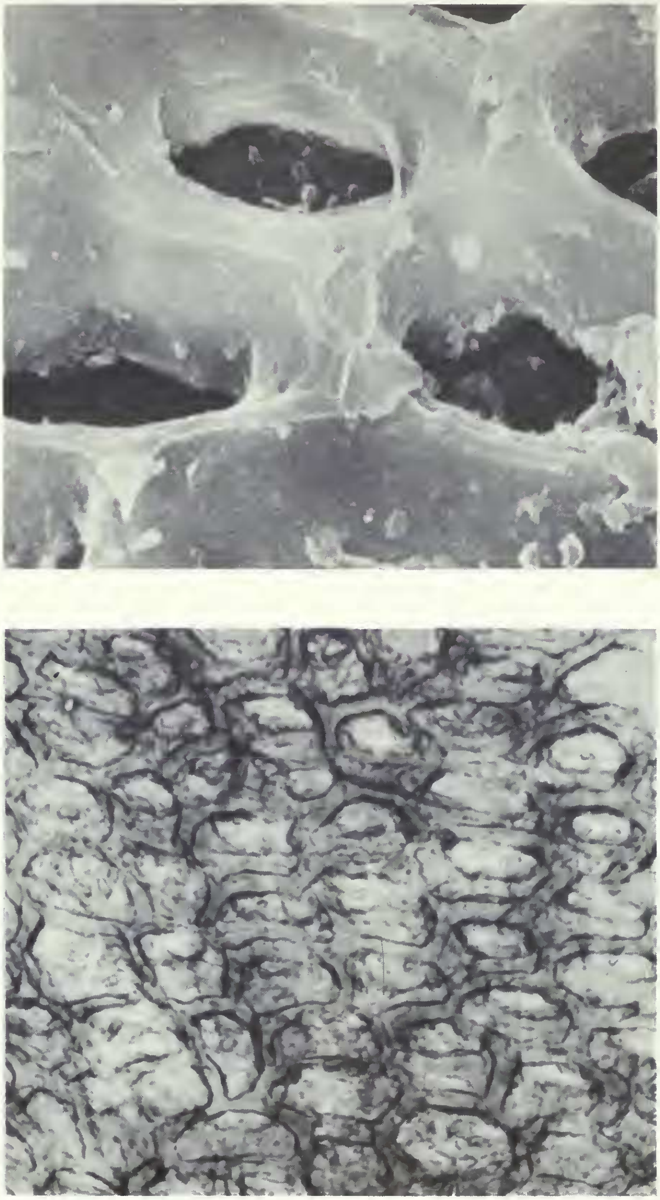

Figs 13–14 *Tomiodendron variabilis*, cuticular material. Fig. 13, stem cuticle from V.42519, ×500. Fig. 14, stem cuticle (view from inner side with scanning electron microscope) of V.42519, ×1500.

Table 1 Comparison of characters of *Tomiodendron variabilis* (Lele & Walton) comb. nov. with described Russian species of *Tomiodendron*.

Species	Phyllotaxy	Shape of leaf cushions	Size of leaf cushions	Infrafoliar bladder	Intercushion distance	Intercushion ornamentation
T. ostrogianum Zalessky, emend. Meyen	Regular orthostichies. Crossing parastichies at 80°–85°	Rhomboidal	7–15 mm long 2–5 mm wide	Linear, 1 mm wide	0·5–2 mm	Striated
T. kemeroviense Chaclov, emend. Meyen	No orthostichies	Lanceolate or narrow elliptical	8–16 mm long 2·5–4 mm wide	Longitudinal fold, 6 mm long, 1·5 mm wide	< 5 mm	Wrinkled
T. asiaticum Zalessky, emend. Meyen	No orthostichies	Oval	7 mm long 3·5 mm wide	Longitudinal fold	< 5 mm	Smooth
T. tetragonum Gorelova	No orthostichies. Crossing parastichies at 20°–40°	Rhomboidal to square	4–7 mm long and wide	–	2–4 mm	Smooth or slightly wrinkled
T. regulare Meyen	Vertical orthostichies	Rhomboidal to oval	7 mm long 2·5–4 mm wide	Central, 0·5–0·7 mm wide	3–4 mm	Finely striated
T. variabilis (Lele & Walton), emend. herein	No orthostichies. Crossing parastichies at 20°–40°	Rhomboidal to oval	Rhomboidal: 5 × 3·5 mm Oval: 2–2·75 mm long 1–1·75 mm wide	Circular, 0·02–0·05 mm wide	0·5–1·5 mm	Smooth

horizontal rows. It also has many stomata on its leaf cushions whereas *Tomiodendron* seems to have none.

Eskdalia has been described as having leaf abscission by Chaloner (1967) and Thomas (1968) but it is now thought to have had persistent leaves (Meyen & Thomas, unpublished). The leaf laminae in *Eskdalia*, however, seem to arise from almost the extreme upper edge of the oval leaf cushions, and the cushions themselves have no infrafoliar bladders.

EMENDED DIAGNOSIS. Stems up to 2 cm broad. Leaves falcate with acute apices, about 1 cm long, attached to ovoidal-rhomboidal leaf cushions measuring up to 5 × 3·5 mm. Ligule pits triangular up to 0·33 mm long with apertures of 0·5 mm. Infrafoliar bladders central and less than one tenth of the maximum width of cushions. Cushion epidermal cells about 30 × 15 μm in size, longitudinally elongated. Stem epidermal cells measuring 30–40 × 15–20 μm, elongated towards leaf cushions.

LECTOTYPE. V.42433, herein selected. Lele & Walton 1962 : pl. 19, figs 1, 2.

LOCALITY. Hazel Hill Quarry, Puddlebrook, Forest of Dean, Gloucestershire, England; National grid ref. SO 646184.

HORIZON. Drybrook Sandstone; lower Upper Viséan.

Acknowledgement

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